

Chihuahuan Desert Soil Biota

Walter G. Whitford¹, Yosef Steinberger^{2*}

¹USDA-ARS Jornada Experimental Range, Box 3JER, New Mexico State University, Las Cruces, NM, USA

²The Mina & Everard Goodman Faculty of Life Sciences, Bar-Ilan University, Ramat Gan, Israel

Email: *Yosef.Steinberger@biu.ac.il

How to cite this paper: Whitford, W.G. and Steinberger, Y. (2021) Chihuahuan Desert Soil Biota. *Open Journal of Ecology*, 11, 581-595.

<https://doi.org/10.4236/oje.2021.119037>

Received: June 18, 2021

Accepted: August 30, 2021

Published: September 2, 2021

Copyright © 2021 by author(s) and Scientific Research Publishing Inc. This work is licensed under the Creative Commons Attribution International License (CC BY 4.0).

<http://creativecommons.org/licenses/by/4.0/>



Open Access

Abstract

Deserts have traditionally been considered as a low moisture system where biological activity is triggered by unpredictable rainfall in time and space. Studies on desert ecosystems functions, processes, dynamics and diversity of soil biota had been found to contribute to understanding of their role in primary production and management of soil ecosystems. As belowground biota is very diverse they are playing an important role in above as well below ground essential ecosystem processes e.g. primary production, decomposition, nutrient mineralization etc. The challenge is to use the emerging knowledge of soil biota diversity in understanding basic ecosystems function.

Keywords

Desert, Soil Biota, Plant Cover, Ecophysiological Adaptation, Plant Soil Biota Interaction

1. Introduction

There are many organisms that fit the category soil biota. In the Chihuahuan Desert the soil biota include: small mammals, subterranean termites, microarthropods, nematodes, protozoans, bacteria, and fungi. In this review the factors limit the activity of each of the organisms, relationship to other species, and the interactions that have an effect on important ecosystem processes such as decomposition and mineralization. The major problem facing anyone with a desire to examine these activities and interactions is lack of taxonomic data for many of the organisms other than insects and mammals. The insects include a variety of ants and subterranean termites. For example there are some keys to genera and species (ants and termites) but for most of the soil biota, taxonomic keys are lacking or for families [1] and sometimes genera of soil nematodes [2]. Despite the lack of taxonomic keys or data, there are numerous aspects of the biology of soil biota

that should warrant attention and allow examination of the role that soil organisms play in the ecosystem.

In the Chihuahuan Desert there are several places where dead plant litter is buried: cache pit excavations, *Yucca elata* logs that result in dams where litter is buried and natural depressions that collect litter. Buried litter forms a substrate for huge range of soil biota communities e.g. (Prostigmatid, Cryptostigmatid, Mesostigmata mites, nematodes collembolans, book lice (Psocoptera), protozoans, bacteria, and fungi. Other soil biota in buried litter include.

2. Biota Composition

2.1. Subterranean Termites

One is not aware of the importance of subterranean termites unless sampled by a variety of baits. We used toilet paper rolls as baits in a grid system to obtain some basic information on termites [3] [4]. We learned that subterranean termites were found in the leaf litter of creosote bushes (*Larrea tridentata*) that had a hemispherical shape. The activity of termites was not different from the inverted cone shaped shrubs and bare ground. The reason for these differences is that shrubs with exterior stem angles of 45° or less do not trap wind-blown litter consisting of leaves, small stems, grass fragments and fragments of herbaceous annuals. Subterranean termites in this desert rarely feed on *L. tridentata* dead leaves [5]. However, subterranean termites prefer fragments of grasses and herbaceous plants and are active in the accumulations of litter under hemispherical shrubs. The advantage of toilet paper rolls as baits is that the roll can be shaken onto a pan and one can record the numbers of termites at that location. Other data that is useful is the percentage of baits that are attacked by termites. We examined the percentage of toilet paper rolls attacked by termites with variable results: *Bouteloua eriopoda* grassland 12% and 60%. *L. tridentata* shrubland 80%, 96%, and 52%. These differences are dependent on the dominant shape of the creosote bushes in the area and the average thickness of the litter layer under the canopy of the shrubs. *Prosopis glandulosa* (mesquite in grassland) 32% and *P. glandulosa* coppice sand dunes 84% (coppice infers stems of relatively the same height emerging from the top of a sand dune. The percentage of baits attacked in tarbush (*Flourensia cernua*) monoculture on clay or clay loam soils 80% and tarbush with burro grass (*Scleropogon brevifolia*) 72%.

Termite grazing accounted for approximately 50% of the mass loss from litter of ephemeral herbaceous plants: *Baileya multiradiata*, *Dasychloa pulchellus*, *Eriastrum diffusum* and *Lepidium lasiocarpum* during the months of maximum surface activity (September and October) in the Chihuahuan Desert [6]. The range of materials consumed is dependent upon the quantity of precipitation and soil temperatures in late summer or early autumn *G. tubiformans* builds gallery carton around the dead wood, ephemeral plants, dead foliage of perennial grasses, dead wood, and dung of large herbivores or mid-size herbivores (Table 1).

Table 1. Termites consume a range of materials based on data from Whitford [7].

Materials	% Removed
Ephemeral plants	40% - 80%
Dead roots-ephemeral plants	50% - 70%
Perennial grass	60% - 90%
Dead grass roots	60% - 70%
Shrub leaves	0% - 90%
Dead wood	<1.0% - 5.0%
Cattle dung	60% - 100%
Rabbit dung	15% - 50%

When the abundance of subterranean termites was estimated based numbers of termites shaken out of toilet paper roll baits mid-slope of a watershed, we estimated the abundance to be 1200 m⁻². During the excavation of a large, 10 meter × 15 meter hole, we recorded termite galleries between 10 meters and 30 meters depth. The termites had produced galleries in the depth of soil to have uniform temperatures even in winter with ambient temperatures less than 0°C.

Unlike earthworms that produce soil aggregates mixed with masticated litter, termites were the only variable in a multiple regression analysis related to soil organic matter. The relationship between termites and soil organic matter was $r = -0.95$. In studies using a rainfall simulation, we found that soils with termites had significantly higher water infiltration rates than soils without termites [8]. That relationship was inferred by the studies of Wood and Sands [9] but not documented. Bulk flow into the foraging tubes of *G. tubiformans* accounts for differences in infiltration. Because subterranean termites affect soil moisture, these insects indirectly affect species composition, and growth rates of the vegetation [10] [11].

In a study using shade and shade plus water, in June, the un-watered soils were at -4 to -6 MPa and the water amended soils were at field capacity. Multiple regression analysis clearly showed that soil moisture at 5 cm depth was the only variable that affected subterranean termite activity and accounted for a large part of the variation in activity of termites [12].

2.2. Ants

Desert seed harvesting ants are an important component of biodiversity in the ant community (*Pogonomyrmex* and *Pheidole*) and are the dominant genera in the Chihuahuan Desert. In a study of colony size and foraging strategies in harvester ants, it was determined that the relationship between colony size and foraging strategy was variable depending upon rainfall, annual grass production and annual herbaceous plant production [13]. Large colonies generally follow trunk

trails that result from pheromones laid down by scouts. Trunk trails are an efficient way to exploit a large quantity of seeds of preferred species but individual foragers that move at random throughout the area are the behavior noted in years when there is little annual grass and herbaceous plant production [14]. There are nine species of seed harvesting ants *P. rugosus*, *P. desertorum*, *P. californicus*, *P. apache*, *P. imberbiculus*, *Ph. desertorum*, *Ph. militicida*, *Ph. rugulosa*, and *Ph. xerophila* that are found in creosotebush dominated areas [15]. There are 3 or 4 species of honey-dew, plant exudates, and insect carrion: *Myrmecocystus depilis/mimicus*, *M. mexicanus*, and *M. navajo*. There is one generalist forager: *Aphenogaster cockerelli*.

We instituted a study of various stressors on the ant communities and the ways in which the ant species responded to different levels of grazing, bull-dozed to level coppice dunes, cover of an exotic grass (Lehmann's lovegrass: *Eragrostis lehmanniana*), grazing exclosures, and areas that had been treated with herbicide in an attempt for the establishment of grasses in place of mesquite coppice dunes (*Prosopis glandulosa*) [16]. We tested hypotheses about the response of several genera of ants: < species richness of *Pheidole* spp., < species richness of *Pogonomyrmex* spp., < species richness of all taxa, > species richness of small ant species: *Dorymyrmex* spp., *Forelius* spp., *Solenopsis* spp., and *Monomorium* spp., < relative abundance of: *Pheidole* spp., *Solenopsis* spp., *Pogonomyrmex* spp., *Pheidole* spp., and of *Myrmecocystus* spp., relative abundance of tolerant species: *Aphenogaster cockerelli*, *Myrmecocystus* spp., *Pogonomyrmex rugosus* (Whitford *et al.* [16]. The highest species richness (38 species) was in an area dominated by the alien grass species (*Eragrostis lehmanniana*). This is in contrast to the native grassland where species richness was only 21 species. That is in comparison to the native grass, *Bouteloua eriopoda*, (30 species of ants) the dominant grass species prior to the introduction of cattle. However, in a creosotebush shrubland dominated landscape the richness of ant species was 26 spp. There were 29 species of ants in an area dominated by tarbush (*Flourensia cernua*). In a shrub-grass mosaic the species richness was 31. The highest relative abundance was frequently shared among species 2nd is the number of habitats with the species: *Aphenogaster cockerelli* (26)(1), *Dorymyrmex insana* (42)(7), *Forelius pruinosus* (52.5)(7), *Myrmecocystus mimicus* (34)(1).

In a study of ants on grassland plots that were paired: shrubs removed and shrubs present, we used a weighted relative abundance consisting of relative abundances of ants: 0 - 6 = 1, 6 - 10 = 2, 11 - 20 = 3, 21 - 30 = 4, 31 - 40 = 5, 41 - 50 = 6 and >50 = 7. The weighted relative abundance was the product of the relative abundance x percent of traps in which a species occurred. The ant community was dominated by *Dorymyrmex insana* with an average weighted abundance of 2488 [17]. The average weighted relative abundance for *Forelius pruinosus* was 478, for *Myrmecocystus depilis* was 164, for *M. mexicanus* was 158, for *Pheidole xerophila* was 158, for *Pogonomyrmex desertorum* was 396, and for *Solenopsis xyloni* was 321. None of the other ants had average weighted relative abundance

< 100. We recorded 27 species in that study with most of the rest of the ants of interest. Among those ants, *Aphenogaster cockerelli*, 8 species of *Pheidole*, 4 species of *Myrmecocystus*, 3 species of *Solenopsis*, and 1 species each of: *Monomorium*, *Camponotus*, *Forelius*, and *Trachymyrmex*. The plots were also grazed by cattle which resulted in homogenized land surface with no mounding [18]. This study showed that cattle hoof action destroyed microtopography but had little effect on the ant fauna of the area.

The studies of ant species richness and diversity miss some of the species that may dominate in a given habitat. For example, *Formica perpilosa*, is associated with tall mesquite at the edges of an ephemeral pond [19] as are the fungus-culturing ant, *Trachymyrmex smithii neomexicanus*. We recorded a relative abundance of *T. smithii neomexicanus* with colonies in the coppice dunes of mesquite and a relative abundance of 2.3. *T. smithii neomexicanus* is dependent upon mesquite leaves as the substrate for culturing fungi on which the ant feeds. The area of coppice dunes of mesquite is very large (>800 km²) with dunes occupying approximately 7 m². The abundance of dunes and the sizes of dunes is the probable cause of the low relative abundance of this ant.

In a creosotebush (*Larrea tridentata*) dominated landscape and the mesquite (*Prosopis glandulosa*) fringe of an ephemeral lake, we recorded three species of large seed harvesters: *Pogonomyrmex rugosus*, *P. desertorum*, and *P. californicus* plus the homopteran tender *Myrmecocystus depilis*, and *M. mexicanus*. One generalist forager, *Aphenogaster cockerelli*, collects insect corpses, leaves, seeds, and flower parts. Two small species: *Dorymyrmex insana*, *Forelius pruinosus* and *D. bicolor* are generalists feeding on honey-dew, small insects and plant exudates. Two small seed feeders: *Solenopsis xyloni* and *Pogonomyrmex imberbiculus* are the other species in this community. There is little overlap among the species in this community and the food items that they collect. (Table 2)

In a study using shade and shade plus water, water alone had a negative effect on three *Pheidole* species (*xerophila*, *rugulosa*, *militicida*) and *Pogonomyrmex desertorum*. Water plus shade had a negative effect on two species (*Ph. xerophila* and *Ph. rugulosa*). Shade alone had a positive effect on *Ph. xerophila* and *Ph. rugulosa* but a negative effect on *P. desertorum*. In the control plots, there was a positive effect on *Ph. xerophila* and *Ph. rugulosa*. In a study of three species of *Pheidole* it was apparent that these species exhibited a seasonal activity with peak activity occurring in July coincident with the onset of summer monsoon rainfall [20]. *Ph. militicida* occurred only on the deeper soils at the base of the watershed while *Ph. rugulosa* and *Ph. xerophila* were found at all elevations on a watershed. The three species of *Pheidole* were most active at sunrise and maintained lower activity at soil surface temperatures between 15°C and 35°C. *Ph. militicida* collected primarily herbaceous annual seeds. *Ph. xerophila* collected mainly grass seeds from fluff grass (*Dasyochloa pulchella*) which is distributed at all elevations on the watershed with the exception of the dry lake at the base of the watershed.

Table 2. Species that inhabit a creosote bush (*Larrea tridentata*) piedmont and the margins of a dry lake. Relative abundance is * for low abundance ** for medium abundance and *** for very abundant. The relative abundance is for the dry lake margin. On the creosote bush piedmont most of the abundances were low. The letters in parentheses are either diurnal (d) nocturnal (n), or both (b).

<i>Pogonomyrmex rugosus</i> (b)***
<i>Pogonomyrmex desertorum</i> (d)***
<i>Pogonomyrmex californicus</i> (d)**
<i>Pogonomyrmex apache</i> (d)*
<i>Pogonomyrmex imberbiculus</i> (d) *
<i>Pheidole desertorum</i> (b)*
<i>Pheidole militica</i> (b)**
<i>Pheidole rugulosa</i> (u)*
<i>Pheidole xerophila</i> (u)**
<i>Mymecocystus depilis/mimicus</i> (d)***
<i>Mymecocystus mexicanus</i> (n)**
<i>Myrmecocystus navajo</i> (u)*
<i>Aphenogaster cockerelli</i> (b)**
<i>Formica perpilosa</i> (d)**
<i>Dorymyrmex bicolor</i> (u)**
<i>Dorymyrmex insana</i> (d)***
<i>Forelius pruinosus</i> (d)**
<i>Solenopsis xyloni</i> (d)***
<i>Solenopsis aurea</i> (u)*
<i>Solenopsis krockowi</i> (u)*
<i>Creumatogaster</i> spp. (n)**
<i>Trachymyrmex smithii</i>
<i>neomexicanus</i> (b)**
<i>Neivamyrmex nigrescens</i> (n)*

2.3. Microarthropods

Most studies of microarthropods utilize a persistent insecticide, chlordane™ in order to evaluate the effects of microarthropods on decomposition of plant materials. The mite fauna is dominated by Prostigmata and not Cryptostigmata (Oribatids) which are dominant in mesic environments. (Table 3)

We studied changes in populations of mites, nematodes, fungi, and bacteria in buried creosote bush (*L. tridentata*) litter with selected inhibitors. Elimination of microarthropods (mostly tydeid mites) resulted in increased numbers of bacteriophagous nematodes and marked reduction in bacteria [22]. Elimination of both nematodes and microarthropods resulted in increased numbers of bacteria compared to untreated controls. Fungal grazing mites (Pyemotidae) and fungivorous nematodes (*Aphelenchus* spp.) increased in numbers between days 25 and 30, reducing the fungi on untreated leaves but not on stems and petioles. Mean length of fungal hyphae increased in insecticide treated leaves. Elimination of mites resulted in a 40% reduction in decomposition. We concluded that in the Chihuahuan Desert, tydeid mites affect the decomposition of buried litter by regulating the population size of bacteria grazing nematodes.

Table 3. The frequency of occurrence of soil microarthropod taxa in soil cores taken each month during a year. Soil cores were taken in a tobosa grass swale (*Pleuraphis mutica*). Taxa with a * are correlated with annual rainfall [21].

Taxon
Acari-Prostigmata
Tydeidae*
Nanochestetidae <i>Spelorchestes</i> spp.*
Linotetranaidae
Pygmephoridae <i>Siteroptes</i> spp.*
Tarsonemidae <i>Tarsonemus fusarii</i> *
Raphignathidae
Stigmaeidae
Bdellidae <i>Spinibdella</i> spp.*
Cunaxidae
Scutacaridae <i>Imparipes</i> spp.*
Trombidiidae
Teneriuffidae
Cryptostigmata-Gymnonota
<i>Passalozetes</i> spp.*
<i>Joshuella</i> spp.*
<i>Cosmocthonius</i> spp.*
<i>Galumna</i> spp.*
<i>Aphelacarius acarinus</i> *
Mesostigmata
Rhodacaridae
Astigmata
Acaridae
Insecta
Diplura (Japygidae)
Psocoptera
Collembola

In a different study, we sampled the role of microarthropods and nematodes in decomposition in the northern Chihuahuan Desert [6]. In that study the mite fauna was dominated by small fungiphagous Pyemotidae, Lordalachidae, and Tarsonemidae in the winter months. In summer, these small fungiphores were replaced as most abundant by a Mesostigmata: Rhodacraidae. Also in summer, there were collembolans and psocopterans in the litter. One interaction that was documented was that Rhodacarid mites fed voraciously on nematodes.

We studied soil microarthropods communities along cattle grazing disturbance from a water point to an area more than one kilometer from the water source. We also examined inside and outside of exclosures to eliminate cattle on the inside of the exclosures. In addition, we sampled areas that had been the subject of restoration efforts: bull dozing and hand applied herbicide to kill mesquite (*P. glandulosa*). We found that mite numbers generally increased from the water point

to the area one kilometer distant from the water point [23]. Soil microarthropods responded to a complex of factors including 1) soil compaction from cattle hoof action at the water point, 2) depth to an impervious soil layer, 3) below-ground vegetative biomass, and 4) residual effects of herbicide. All cores except those that were herbicide treated were dominated by Nanorchestidae.

In all of the cores, numbers of mites-core⁻¹ of the family Nanorchestidae dominated the disturbances. Total numbers of Nanorchestids were identified: bulldozed-60, bulldozed control-75, grazed-23, exclosure-64, hand sprayed herbicide-5, hand-sprayed control-68, aerial spray-40, aerial spray control-98. Other mites included Tarsonemidae < 20 core⁻¹ except in the aerial sprayed plots at 20 core⁻¹. In this experiment, Tydeid mites ranged between 5 and 15 core⁻¹.

Most of the samples were collected during a year that was characterized by 47% below average precipitation. The soils at water points were mixed by cattle with cattle dung mixed into the surface layer. There was a compacted layer at 10 to 15 cm below the well mixed layer with very few microarthropods.

In a study of one year duration and with roots and aboveground litter of a spring annual (*Lepidium lasiocarpum*), the most abundant microarthropods were tydeid mites during the early stages of decomposition [24]. Tydeid populations declined rapidly and by day 96 contributed little to the microarthropod population. By day 32 the fungus-feeding tarsonemid mites appeared and they maintained high populations to the end of the study. The differences of microarthropod populations between roots and litter were that mesostigmatid appeared sooner in litter than in roots. The other difference was that by day 56 tarsonemid mites were an order of magnitude higher in litter than in roots. Parker *et al.* [24] suggested that microarthropods are important in uncoupling the system from abiotic parameters. Coleman *et al.* [25] showed that protozoans and nematodes are important regulators of nitrogen mineralization in the absence of fungi and higher trophic groups.

In a study of rainfall supplement (25 mm-month⁻¹ and 6 mm-week⁻¹) on microarthropods associated with decomposing roots of woody shrubs and spring herbaceous annuals, we were able to identify several mites to genus: *Tydeus* spp., *Speleorchestes* sp., *Tarsonemus* sp., Pygmephoridae—*Siteroptes* sp., and two Cryptomatids: *Passalotes* spp. and *Cosmocthonius* sp. [26]. The taxa associated with decomposing roots were the same taxa that were isolated from litter bags containing a mix of grasses and herbaceous annuals.

2.4. Nematodes

The genera of nematodes were based on the feeding habits or stoma and esophageal morphology. Nematodes were identified to genus according to the following groups 1) herbivore, 2) fungivore/fungus feeder, 3) bacteria feeders and 4) omnivore-predators according to Yeates *et al.* [2].

In a study of controlled burns on free-living nematodes there were 21 genera of bacteria feeders, six genera of fungivores, 15 genera of plant parasitic nema-

todes, and 13 genera of omnivore-predators [27]. Fire can affect the physical, chemical and biological properties of soil, *i.e.* aggregate stability, pore size distribution, water repellency, bulk density, decomposer/mineralization rates, food web modification, modification of mineralization rates, carbon sequestration, microbial species composition and nutrient availability [28]. The data are for several months post-burn and unburned patches of *Juniperus monosperma* and *Yucca baccata*. When the nematode community is broken down by trophic levels, the bacteria feeders accounted for 21 of the 55 genera of nematodes. Fungivores accounted for only 6 of the genera, plant parasitic nematodes accounted 15 genera and omnivore/predators accounted for 13 of the genera. The dominant genera were nematodes that accounted for at least 1 core⁻¹ from the *Yucca baccata* or *J. monosperma* patches (Table 4).

Nematode biomass around the fungicide-insecticide treated roots increased by four orders of magnitude by day 56. At the end of the experiment nematode biomass associated with roots was higher than the biomass associated with litter [24]. In addition there were other mites with an average per core of less than one: Nanorchestidae, Bdellidae, Pyemotidae and Cunaxidae. There was one Mesostigmata, a predator, with an average population in litter bags containing *L. lasiocarpum* above ground parts and roots of 37 ± 14 . Collembolans did not enter the mesh bags until day 96 and these were fungivorous collembolans: Isotomidae.

Table 4. Nematode genera that appeared in core samples (average number per core) from burned and unburned patches of *Yucca baccata* and *Juniperus monosperma*.

	<i>Juniperus monosperma</i>		<i>Yucca baccata</i>	
	burned	unburned	burned	unburned
Bacteria Feeders				
<i>Acrobeles</i> spp.	42.7	46.6	27.8	37.2
<i>Acroboloides</i> spp.	11.1	4.4	16.3	0
<i>Cervidellus</i> spp.	10.4	0.3		
<i>Chiloplacus</i> spp.	8.1	2.1	29.6	19.7
<i>Eucephaloides</i> spp.	26.1	19.9	35.7	5.8
<i>Panagrolaimus</i> spp.	22.5	0.6	4.0	6.0
<i>Tylocephalus</i> spp.	3.5	0.2	-	-
<i>Prismatolaimus</i> spp.	2.3	0.2	4.0	0.5
Fungivores				
<i>Aphelenchoides</i> spp.	6.3	14.2	5.8	1.0
<i>Aphelenchus</i> spp.	5.2	0.6	0.1	0.9
Plant Parasites				
<i>Filenchus</i> spp.			6.8	0.4
Omnivore/Predator				
<i>Aporcelaimus</i> spp.	6.0	1.7	45.8	18.6
<i>Microdorylaimus</i> spp.	1.6	11.9	6.9	4.1

2.5. Protozoans

We designed a study of protozoans associated with the nests of one species known to have an effect on the plants around the nest site [29] and two species of ants known not to be seed harvesters: *Myrmecocystus depilis* and *Aphaenogaster cockerelli*. *M. depilis* tend homopterans for honey-dew, and collect small insects. *A. cockerelli* is a generalist forager that collects dead insects, plant parts, and seeds. We recorded the morphological types of amoebae as proposed by [30] as follows: type 1 flattened amoebae bearing sub-pseudopodia (like acantaamoeba; type 2 slender and cylindrical amoebae with a long non-eruptive pseudopodium (like *Hartmannella*); type 3 eruptive, triangular shape with a wide lobopodium (like Vahlkampfiidae); type 4 fan shaped amoebae like Platyamoebidae and Vannelliidae. We concluded that the protozoan community associated with ant nests varies both qualitatively and quantitatively with ant species, topographic position, and soil properties.

Protozoans were more abundant in the *A. cockerelli* nest soils than in the reference soils but there were no differences in abundance of protozoans associated with *P. rugosus* soils [31]. The *A. cockerelli* provided habitat for all eight types of protozoans recognized in this study. There were significantly more flagellates in *M. depilis* modified soils than in reference soils. Nest soils of *P. rugosus* supported testate amoebae which were absent from reference soils. Ciliates were isolated from reference soils at the top of the catena but not from the nest soils of the ant species. The protozoan community in the *P. rugosus* nest soils supported ciliates. The protozoan assemblage consisted of type 4 amoebae, and testate amoebae in the reference soils but not in the nest soils.

In a study of protozoans living in the soil around ant nests located in a grassland and on a low sloping catena, we found that the highest number of protozoans was in soils around *Pogonomyrmex rugosus* nests and in the soil of *Aphaenogaster cockerelli* nests in the grassland. Total protozoan abundance was in *P. rugosus* soils at the margin of the nest at the top of the catena [31]. There were both qualitative and quantitative differences in protozoans in nest modified soils and in reference soils. Amoebae were the most abundant form in all nest modified soils and in some reference soils depending upon location on a catena. Type 1 amoebae (flattened with sub-pseudopodia like *Acanthamoeba*) occurred at the highest frequency and was the only type of amoebae found in *Myrmecocystus depilis* nest soils and *P. rugosus* nest soils at the top of the catena. Nanoflagellates were associated with *P. rugosus* nest soils and *A. cockerelli* nest soils but were absent from the reference soils. Ciliates, testate amoebae, and nanoflagellates were absent from *A. cockerelli* reference soils but were present in the nest modified soils.

2.6. Microorganisms

In one study, we examined the microbial biomass and diversity in soils modified by the nests of ants that persist in the environment for more than a decade. Only

one of the three species studied (*Pogonomyrmex rugosus*) exhibited higher microbial biomass than reference soils > 3 m away from the focal nest. There were no differences in microbial biomass in the nest soils of the other two species, (*Aphenogaster cockerelli* and *Myrmecocystus depilis*) in comparison with the reference soils. There were differences in microbial functional diversity and microbial community level physiological profiles between ant nest modified soils and reference soils [32]. Temporal patterns of soil microbial communities associated with ant nests resulted from differences in soil moisture plus differences in species composition and biomass of annual plants associated with the nests or reference sites [33]. The seed harvester-ant chaff piles at the margins of the nest provided the organic carbon required for higher growth rates of the microbial populations. However, when effective rainfall was low or absent, the differences among ant nests and reference soils either disappeared or was reversed. This result questions the studies of a single season with differences between nest soils and microbes because during an extended dry period, the results may be different [34].

In a study that examined the effects of intense grazing by cattle, seasonal drought, and fire on soil microbial diversity (substrate utilization) and activity in a Chihuahuan Desert grassland over a full year [35]. Microbial diversity was estimated from carbon substrate utilization patterns in both gram + and gram - Biolog plates. Neither microbial diversity nor microbial activity was affected by livestock grazing. Burning reduced microbial diversity and most enzyme activities compared to controls in summer and spring. The maximum microbial activity and diversity occurred only in the summer-drought stress sub-plots than in the control sub-plots in summer and spring. Microbial diversity was highest in summer, intermediate in winter and lowest in spring. In the Chihuahuan Desert spring is the driest season. Substrate availability was the most important factor affecting the diversity and activity of soil microorganisms within a season. Soil moisture was not the factor affecting microbial diversity and activity among the stress treatments but it was a predictor for some microbial responses under a particular stress [35].

Total soil respiration is an important ecosystem attribute that provides an estimate of the turnover of soil organic matter. Soil respiration results from the activity of soil microbes, soil animals, and roots [36]. Coleman [36] suggested that 45% of the root respiration probably resulted from rhizosphere microflora, therefore only 3% - 9% was attributable to roots. In our study, soil respiration was highest in July and August concomitant with the summer monsoon rainfalls. Soil organic matter turnover was estimated at 20.7 years based on the annual precipitation. Soil respiration had an optimum temperature of 41°C in both wetted (addition of 254 mm via sprinklers) and dry soil. This value must be interpreted with caution since Chihuahuan Desert soils are still undergoing change resulting from a major shift from grassland to shrub dominated ecosystems. Approximately 71% of the CO₂ output was attributed to microbes (bacteria and fungi) reinforcing the idea that soil microorganisms are responsible for most of the soil

Table 5. Average frequency of fungi found on creosotebush wood with or without the action of subterranean termites.

<i>Alternaria alternata</i>	9 ± 2
Basidiomycete	6 ± 2
<i>Colephoma</i> spp.	84 ± 4
Coniothyrium spp.	43 ± 27
<i>Fusarium acuminatum</i>	14 ± 20

respiration. Soil respiration was between 200 and 360 mg (CO₂) m⁻²·h⁻¹ in May through July. There was a peak in soil respiration of 600 mg·m⁻²·h⁻¹ coincident with the peak rainfall in August of 40 mm (long-term average rainfall for this area is 250 mm·y⁻¹).

There are several genera of fungi and termite species that work on dead creosote bush wood (Table 5). Dead wood can be a significant component of the total carbon pool and an important nutrient sink in desert ecosystems.

3. Biopedturbation

One aspect of several of the larger soil organisms is biopedturbation. Biopedturbation is defined as anything that disrupts the soil surface and increases sediment yields from desert watersheds [37]. We recognize pocket gophers as agents of biopedturbation but fail to recognize the actions of small rodents in digging cache pits to recover seeds and potentially in digging cache pits to store seeds [38]. Small ants e.g. (*Dorymyrmex insana*) produce piles of excavated soil around the entrance to the nest. Subterranean termites build gallery carton around stems of plants in order to consume the dead herbaceous plants. Gallery carton is also found within clumps of perennial grasses and on dead stems of shrubs. Not all excavations are small. Badgers dig out honey pot ant (*Myremcosystus* spp.) to obtain water and sweets (the gaster of the ants is called a honey pot) leaving a large pit more than a meter in diameter and a meter or more in depth. Large-deep excavations accumulate litter and soil from the excavation pile. These excavations combined with the rodent cache pits are important sources of nutrient heterogeneity in the soil.

4. Soil Biodiversity

In a discussion of the likely determinants of soil biota diversity [39] and ecosystem function, Bardgett [39] infers that there is little evidence that soil biodiversity is regulated in a predictable fashion by competition or disturbance. It is attributed to soil heterogeneity both spatially and temporally. In the Chihuahuan Desert there is evidence of soil heterogeneity affecting biodiversity but also evidence that predation and competition are processes that affect biodiversity.

Summary

In this report we have demonstrated that ecosystem processes are regulated by one or two species. We have evidence that in desert soils there is no redundancy

as suggested by Bardgett [39]. There is a succession of species that breaks down dead plant materials and that seems to be the primary process in the soil. There is a diverse set of organisms that regulate decomposition (an essential process to release nutrients from organic debris). Their appearance appears to be associated with the microorganisms that attack the debris at fixed intervals.

Acknowledgements

The authors would like to thank to especially Prof. John A. Wallwork for his friendship and his valuable contribution in the field of soil ecology. We would like to thank as well to many students and workers in field of soil ecology who contributed in data acquisition and to our understanding in desert ecosystem function.

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

References

- [1] Krantz, G.W. (1978) Manual of Acarology. 2nd Edition, Oregon State Book Stores Inc., Corvallis.
- [2] Yeates, G.W., Bongers, T., DeGroede, R.G.M., Freckman, D. and Georgieva, S.S. (1993) Feeding Habits in Soil Nematode Families and Genera: An Outline or Soil Ecologists. *Journal of Nematology*, **25**, 315-331.
- [3] LaFage, J.P., Nutting, W.L. and Haverty, M. (1973) Desert Subterranean Termites: A Method for Studying Foraging Behavior. *Environmental Entomology*, **2**, 954-956. <https://doi.org/10.1093/ee/2.5.954>
- [4] Johnson, K.A. and Whitford, W.G. (1975) Foraging Ecology and Relative Importance of Subterranean Termites in a Chihuahuan Desert Ecosystem. *Environmental Entomology*, **4**, 66-70. <https://doi.org/10.1093/ee/4.1.66>
- [5] Fowler, H.G. and Whitford, W.G. (1980) Termites, Microarthropods and the Decomposition of Senescent and Fresh Creosotebush (*Larrea tridentata*) Leaf Litter. *Journal of Arid Environments*, **3**, 63-68. [https://doi.org/10.1016/S0140-1963\(18\)31675-6](https://doi.org/10.1016/S0140-1963(18)31675-6)
- [6] Elkins, N.Z. and Whitford, W.G. (1982) The Role of Microarthropods and Nematodes in Decomposition in a Semi-Arid Ecosystem. *Oecologia*, **55**, 303-310. <https://doi.org/10.1007/BF00376916>
- [7] Whitford, W.G. (1991) Subterranean Termites and Long-Term Productivity of Desert Rangelands. *Sociobiology*, **19**, 235-243.
- [8] Elkins, N.Z., Sabol, V., Ward, T.J. and Whitford, W.G. (1986) The Influence of Subterranean Termites on the Hydrological Characteristics of a Chihuahuan Desert Ecosystem. *Oecologia*, **56**, 521-528. <https://doi.org/10.1007/BF00378766>
- [9] Wood, T.G. and Sands, W.A. (1978) The Role of Termites in Ecosystems. In: Brian, M.V., Ed., *Production Ecology of Ants and Termites*, Cambridge University Press, Cambridge, 245-282.
- [10] Gutierrez, J.R. and Whitford, W.G. (1987) Chihuahuan Desert Annuals: Importance of Water and Nitrogen. *Ecology*, **58**, 2032-2045. <https://doi.org/10.2307/1939894>

- [11] Gutierrez, J.R. and Whitford, W.G. (1989) Effect of Eliminating Subterranean Termites on the Growth of Creosotebush, *Larrea tridentata*. *The Southwestern Naturalist*, **34**, 549-561. <https://doi.org/10.2307/3671517>
- [12] Mackay, W.P., Silva, S., Lightfoot, D.C., Pagani, M.I. and Whitford, W.G. (1986) Effect of Increased Soil Moisture and Reduced Soil Temperature on a Desert Soil Arthropod Community. *American Midland Naturalist*, **16**, 45-56. <https://doi.org/10.2307/2425936>
- [13] Warburg, I., Whitford, W.G. and Steinberger, Y. (2017) Colony Size and Foraging Strategies in Desert Seed Harvester Ants. *Journal of Arid Environments*, **145**, 18-23. <https://doi.org/10.1016/j.jaridenv.2017.04.016>
- [14] MacMahon, J.A., Moll, J.F. and Crist, T.O. (2000) Harvester Ants (*Pogonomyrmex* spp.). *Annual Review of Ecology and Systematics*, **31**, 2656-291. <https://doi.org/10.1146/annurev.ecolsys.31.1.265>
- [15] Whitford, W.G. (1978) Structure and Seasonal Activity of Chihuahuan Desert Ant Communities. *Insectes Sociaux*, **25**, 79-88. <https://doi.org/10.1007/BF02224487>
- [16] Whitford, W.G., Van Zee, J., Nash, M.S., Smith, W.E. and Herrick, J.E. (1999) Ants as Indicators of Exposure to Environmental Stressors in North American Desert Grasslands. *Environmental Monitoring and Assessment*, **54**, 143-171. <https://doi.org/10.1023/A:1005858918860>
- [17] Nash, M.S., Whitford, W.G., Van Zee, J. and Havstad, K.M. (2000) Ant (Hymenoptera: Formicidae) Responses to Environmental Stressors in the Northern Chihuahuan Desert. *Environmental Entomology*, **29**, 200-206. <https://doi.org/10.1093/ee/29.2.200>
- [18] Nash, M.S., Jackson, E. and Whitford, W.G. (2003) Soil Microtopography on Grazing Gradients in Chihuahuan Desert Grasslands. *Journal of Arid Environments*, **55**, 181-192. [https://doi.org/10.1016/S0140-1963\(02\)00251-3](https://doi.org/10.1016/S0140-1963(02)00251-3)
- [19] Schumacher, A. and Whitford, W.G. (1974) The Foraging Ecology of Two Species of Chihuahuan Desert Ants: *Formica perpilosa* and *Trachymyrmex smithi neomexicanus* (Hymenoptera: Formicidae). *Insectes Sociaux*, **21**, 317-330. <https://doi.org/10.1007/BF02226923>
- [20] Wisdom, W.A. and Whitford, W.G. (1981) Effects of Vegetation Change on Ant Communities of Arid Rangelands. *Environmental Entomology*, **10**, 893-897. <https://doi.org/10.1093/ee/10.6.893>
- [21] Steinberger, Y. and Whitford, W.G. (1985) Microarthropods of a Desert Tabosa Grass (*Hilaria mutica*) Swale. *American Midland Naturalist*, **114**, 225-234. <https://doi.org/10.2307/2425598>
- [22] Santos, P.F., Phillips, J. and Whitford, W.G. (1981) The Role of Mites and Nematodes in Early Stages of Buried Litter Decomposition in a Desert. *Ecology*, **62**, 664-669. <https://doi.org/10.2307/1937734>
- [23] Kay, F.R., Sobhy, H.M. and Whitford, W.G. (1999) Soil Microarthropods as Indicators of Exposure to Environmental Stress in Chihuahuan Desert Rangelands. *Biology and Fertility of Soils*, **28**, 121-128. <https://doi.org/10.1007/s003740050472>
- [24] Parker, L.W., Santos, P.F., Phillips, J. and Whitford, W.G. (1984) Carbon and Nitrogen Dynamics during the Decomposition of Litter and Roots of a Chihuahuan Desert Annual, *Lepidium lasiocarpum*. *Ecological Monographs*, **54**, 339-360. <https://doi.org/10.2307/1942501>
- [25] Coleman, D.C. anderson, A.V., Cole, E.T., Elliot, E.T., Woods, L. and Campion, M.K. (1978) Trophic Interactions in Soils as They Affect Energy and Nutrient Dynamics IV. Flows of Metabolic and Biomass Carbon. *Microbial Ecology*, **4**, 373-380.

- <https://doi.org/10.1007/BF02013280>
- [26] Whitford, W.G., Stinnet, K. and Steinberger, Y. (1988) Effects of Rainfall Supplementation on Microarthropods on Decomposing Roots in the Chihuahuan Desert. *Pedobiologia*, **81**, 147-155.
- [27] Whitford, W.G., Pen-Mouratov, S. and Steinberger, Y. (2014) The Effects of Prescribed Fire on Soil Nematodes in an Arid Juniper Savanna. *The Open Journal of Ecology*, **4**, 66-75. <https://doi.org/10.4236/oje.2014.42009>
- [28] Doerr, S.H. and Cerda, A. (2005) Fire Effects on Soil System Functioning: New Insights and Future Challenges. *International Journal of Wildland Fire*, **14**, 339-342. <https://doi.org/10.1071/WF05094>
- [29] Whitford, W.G. and Duval, B.D. (2019) Ecology of Desert Systems. Academic Press, Cambridge.
- [30] Anderson, O.R. and Rogerson, A. (1995) Annual Abundances and Growth Potential of Gymnamoebae in the Hudson Estuary with Comparative Data from the Firth of Clyde. *European Journal of Protistology*, **31**, 223-233. [https://doi.org/10.1016/S0932-4739\(11\)80446-3](https://doi.org/10.1016/S0932-4739(11)80446-3)
- [31] Zaragoza, S.R., Whitford, W.G. and Steinberger, Y. (2007) Effects of Temporally Persistent Ant Nests on Soil Protozoan Communities and the Abundance of Morphological Types of Amoeba. *Applied Soil Ecology*, **37**, 81-87. <https://doi.org/10.1016/j.apsoil.2007.04.002>
- [32] Whitford, W.G., Ginzberg, O., Berg, N. and Steinberger, Y. (2012) Do Long-Lived Ants Affect Soil Microbial Communities. *Biology and Fertility of Soils*, **48**, 227-233. <https://doi.org/10.1007/s00374-011-0619-4>
- [33] Zak, J.C., Willig, M.R., Moorhead, D.L. and Wildman, H.G. (1994) Functional Diversity of Microbial Communities: A Quantitative Approach. *Soil Biology and Biochemistry*, **26**, 1101-1108. [https://doi.org/10.1016/0038-0717\(94\)90131-7](https://doi.org/10.1016/0038-0717(94)90131-7)
- [34] Boulton, A.M., Jaffee, B.A. and Scow, K.M. (2003) Effects of a Common Harvester Ant (*Messor andrei*) on Richness and Abundance of Soil Biota. *Applied Soil Ecology*, **23**, 257-265. [https://doi.org/10.1016/S0929-1393\(03\)00046-5](https://doi.org/10.1016/S0929-1393(03)00046-5)
- [35] Liu, X., Lindemann, W.C., Whitford, W.G. and Steiner, R.L. (2000) Microbial Diversity and Activity of Disturbed Soil in the Northern Chihuahuan Desert. *Biology and Fertility of Soils*, **32**, 243-249. <https://doi.org/10.1007/s003740000242>
- [36] Coleman, D.C. (1973) Compartmental Analysis of "Total Soil Respiration" an Exploratory Study. *Oikos*, **24**, 361-366. <https://doi.org/10.2307/3543811>
- [37] Whitford, W.G. and Kay, F.R. (1999) Biopedturbation by Mammals in Deserts: A Review. *Journal of Arid Environments*, **41**, 203-220. <https://doi.org/10.1006/jare.1998.0482>
- [38] Eldridge, D.J. and Whitford, W.G. (2009) Badger (*Taxidea taxa*) Disturbances Increase Soil Heterogeneity in a Degraded Shrub-Steppe Ecosystem. *Journal of Arid Environments*, **73**, 66-73. <https://doi.org/10.1016/j.jaridenv.2008.09.004>
- [39] Bardgett, R.B. (2002) Causes and Consequences of Biological Diversity in Soil. *Zoology*, **105**, 367-375. <https://doi.org/10.1078/0944-2006-00072>